THE SYSTEMATIC AND PHYLOGENETIC POSITION OF *PALAEOSPONGILLA CHUBUTENSIS* (PORIFERA : SPONGILLIDAE)

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Synopsis

Palaeospongilla chubutensis Ott and Volkheimer (1972), the first fossil spongillid ever recorded, was detected during an examination of stromatolithic crusts of blue-green algae from lacustrine sediments of the Cretaceous of Patagonia. It is represented by a fully intact skeletal arrangement of megascleres and microscleres, both of two types, and also contains numerous gemmules with gemmoscleres *in situ*.

Based on a thorough reexamination of parts of the type material, which demonstrates the early perfection of gemmule-producing freshwater Demospongiae, the present study reveals additional criteria which are used to interpret more precisely the relationship of the Mesozoic fossil to extant genera and species. *P. chubutensis* displays gemmoscleral characteristics from which both acerate and birotulate spicular types could have evolved by divergence, and it is significant to find it the almost direct ancestral form of the extant genus *Radiospongilla* which has retained identical gemmular and gemmoscleral criteria and which today represents such a central stock. Furthermore, the fossil spongillid is obviously closely related to two additional extant genera, i.e. *Spongilla* and *Pectispongilla*, which also share some of its structural characteristics.

Recent advances in the fields of palaeolimnology, plate tectonics, and continental drift provide a feasible background for speculation on spongillid evolution, dispersal routes and distribution since the occurrence of the Patagonian fossil, some 100 million years ago.

Introduction

The discovery of extensive fully fossilised crusts of the spongillid *Palaeospongilla chubutensis* in lacustrine sediments of the Cretaceous in the Chubut River Valley of Patagonia, by Ott and Volkheimer (1972), can only be described as exciting. Although spicular remains of freshwater Porifera, mostly comparable with those of extant genera and species, have been recorded from a number of lentic sediments of Tertiary age (Traxler, 1895, 1896 ; Reul, 1954 ; Racek, 1966, 1969, 1970), no palaeontological evidence could hitherto be obtained for Mesozoic occurrences of gemmule-producing freshwater Demospongiae, nor was it considered likely that a well-preserved spongillid fossil could ever be found. Factors preventing successful fossilisation of freshwater sponges would seem to include both their comparatively flimsy skeleton, and, in particular, the established rapid deterioration of their symplasm after death. The exceptionally perfect preservation of *P. chubutensis*, over a period of more than 100 million years, can thus only be explained by the fact that its entire surface was rapidly covered by a thick layer of calcareous algae (Cyanophyceae) which smothered the sponge itself and simultaneously prevented it from being crushed during sedimentation.

Realising the uniqueness of their unexpected discovery, made during a routine examination of stromatolithic crusts of blue-green algae, Ott and Volkheimer (1972) proceeded with the description of *P. chubutensis*, which they rightly considered generically and specifically different from any extant spongillid hitherto recorded. However, in spite of the clarity and morphometric accuracy of the original description, the present authors considered it imperative to reexamine parts of the type material in order to attempt a reliable assessment of the fossil's systematic and phylogenetic position in line with the recent comprehensive revision of Penney and Racek (1968), which was unavailable to the describing palaeobotanists. This reexamination, made possible by courtesy

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of Dr. E. Ott, revealed additional information of multidisciplinary significance, which enabled the present authors to solve a number of problems previously encountered.

Material and Methods

The fossilised remains of *P. chubutensis*, used for this study, consisted of three slides containing thinly ground sections of a topotype, i.e. material adjoining that selected as a holotype by Ott and Volkheimer. Although these sections permitted most useful general observations, and were at least as informative as the slides used for the original description of the sponge, it became necessary to separate the various spicules from the rocky matrix so that their detailed structures could be thoroughly examined. This was first achieved by removing the mounting medium of the slides with xylene and acetone, after which the matrix was treated with boiling nitric acid in order to dissolve all non-siliceous matter and to reveal the structural characteristics of the spicules. The illustrations for this paper were prepared from photomicrographs and camera lucida drawings, using a Zeiss-Winkel microscope and its accessories.

Revised Morphological Evaluations

Palaeospongilla chubutensis Ott and Volkheimer, 1972, pp. 49–63.

Holotype. Three sections and one polished rest-cut of the branch holding the sponge incrustation, in the collections of the Museo Argentino de Ciencias Naturales " B. Rivadavia ", Buenos Aires.

Topotype (selected by the present authors). Three sections from another part of the fossil, of which one was fully dissolved in nitric acid, resulting in several spicule slides ; material deposited in part in the collections of the Australian Museum, Sydney, and in part in those of the Smithsonian Institution, U.S. National Museum, Washington, D.C.

Type locality. Cretaceous lacustrine sediments of the Chubut Group, Valley of the Rio Chubut, 16 km NNW of Cerro Condor, Patagonia, Argentina.

Distribution. Hitherto known only from the type locality.

Redescription. Sponge encrusting the fossilised remains of what appears to be a gymnosperm stem or root, in cushions from 2 to 6 mm in thickness, and surrounded by a rather thick layer of covering calcareous algae (Cyanophyceae). Skeleton forming several clearly defined tiers of megascleres, displaying a well-arranged and rather regular meshwork of vertical and horizontal spicule fibres, indicating the original presence of a considerable amount of binding spongin. Spicule fibres consisting of joined bundles of up to 40 megascleres, forming meshes of about 1000 μm in diameter. Original surface of sponge difficult to assess since the surrounding thick crust of calcareous algae adjoins very closely.

Megascleres of two distinct types, both feebly curved or almost straight. The much more common type A represented by rather stout and almost cylindrical amphioxea, as a rule completely smooth, occasionally bearing one or two irregular smaller spines without characteristic arrangement or position (Fig. 1a). Length range 420–540 μm, width range 10–22 μm. Megascleres of type B less prevalent in the preparations made, smaller and more slender, typically fusiform with rather sharp apices, armed with inconspicuous spines except at their tips (Fig. 1b). Length range 180–308 μm, width range 4–14 μm. Megascleres of type A forming the main skeleton of basal and central parts of the sponge, those of type B associated more with peripheral spicule fibres.

Free microscleres (Fleischnadeln), like the megascleres, of two distinct types, both almost straight or only very slightly curved amphioxea with distinctly sharp apices. The much more common type A represented by rather long and slender scleres, incipiently to conspicuously spined along almost their entire length (Fig. 1c). Length range 179–190 μm (partly assessed from fragments), width range 3–4 μm, spines rarely exceeding 1μm in height. Microscleres of type B somewhat smaller and entirely smooth amphioxea (Fig. 1d). Length range 77–147 μm (partly assessed from fragments), width range 3–5 μm. Both types seem not to be indicative of a certain position in the sponge, although they appear more abundant above the layer of gemmules.

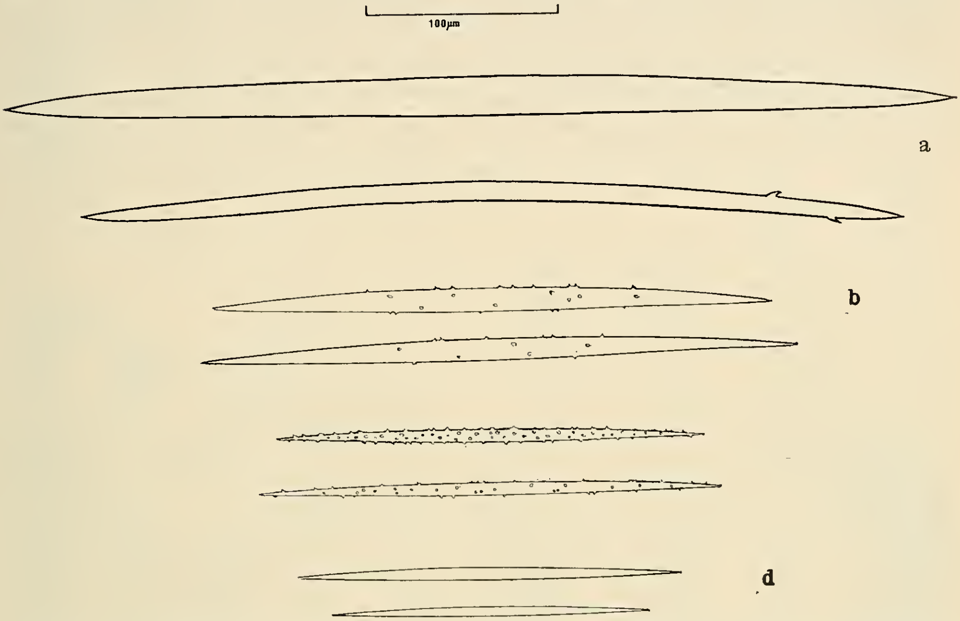

Fig. 1. *Palaeospongilla chubutensis.* a. Range of megascleres of type A. b. Range of megascleres of type B. c. Range of microscleres of type A. d. Range of microscleres of type B.

Gemmoscleres moderately long and slender amphistrongyla, often possessing a spine in the prolongation of their axis so that they appear amphioxeous. They are armed with numerous acute spines along their entire shaft, while in the vicinity of the extremities of the sclere these spines are distinctly aggregated, often forming sceptre-like distal arrangements of perceptibly recurved teeth (Fig. 2a). Pseudorotules could not be observed. Length range of gemmoscleres, which are only slightly curved, 77–168 μm, width range 3·5–6 μm.

Gemmules quite abundantly produced, not confined to base of sponge but instead freely scattered through skeletal meshwork. Although they are generally spherical, ranging in diameter 490–570 μm, their thick and well-developed pneumatic coat is of irregular height, varying from 63 to 95 μm (Fig. 2b). Gemmoscleres embedded in this coat more or less radially but mostly crossing each other at various angles, arranged in one layer only, their distal extremities not appreciably penetrating the outer gemmular membrane. None of the sections available displayed a cut through the region of the micropyle ; thus foraminal structures remain unknown.

Discussion. Ott and Volkheimer (1972), the discoverers of this first spongillid known from the Mesozoicum, provided a very useful general description and carefully assessed measurements of the variety of spicular components. However, some of their morphological evaluations must now be amended. Since they had no access to recent taxonomic revisions (Penney and Racek, 1968; Racek, 1969, 1970), which include data from subfossil spicular remains, and based their description on the study of thin sections only, it is understandable that they faced difficulties in expressing the status of some scleral components. While the megascleres of type A, including those which possess a small number of irregular spines, were correctly observed, the spined type B were not recognised as megascleres, but were instead included in the range of occurring free microscleres, thus indicating a greater average length of the latter. The assessment of all scleres from sections, the matrix of which grossly distorts the

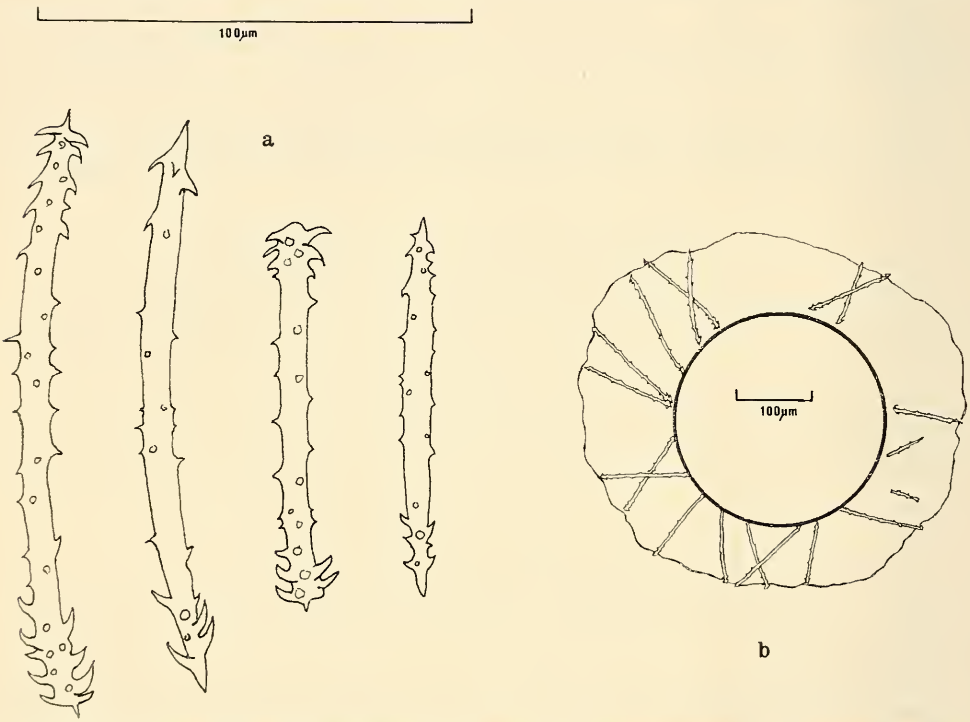

Fig. 2. *Palaeospongilla chubutensis*. a. Range of gemmoscleres. b. Section through fossilised gemmule, with gemmoscleres *in situ*.

characteristics of the spicules, seems to have resulted in somewhat misleading line drawings, which show little resemblance to those scleres illustrated in the excellent photomicrographs of the original description. Following the isolation, by the present authors, of spicular components from the matrix, it can now be established that there are two types of both megascleres and microscleres, a condition which has not been retained in any extant genus of the now redundant subfamily Spongillinae Vejdovsky, i.e. those spongillids possessing acerate (non-birotulate) gemmoscleres. The possibility of a spicular mixture of two distinct species, both fossilised simultaneously, can be readily dismissed. Although such a condition can occasionally be observed in living spongillids (usually a result of competition for a restricted substrate), there is always evidence of growth overlap, i.e. two distinctly separated skeletal floors, each displaying the spicular characteristics of one of the adjoining or overgrowing spongillids involved. The careful examination of the skeletal arrangement of *P. chubutensis* did not reveal such a condition and demonstrated beyond doubt that the spicular components of the fossil belong to a single species. Both types of megascleres take part in the construction of a rather uniform skeleton, uninterrupted by membranes, tiers or floors. The free microscleres of both types occur side by side throughout the quite insignificant height of the sponge crust, without any indicative position. The typical gemmules are not restricted to either the upper or lower portion of the flat sponge growth but are scattered throughout the skeletal meshwork. No other types of gemmules nor even single gemmoscleres of any other species could be observed in the material available.

Considering all the morphological characteristics of *P. chubutensis*, as reexamined by the present authors, and in spite of the close affinities of both gemmules and gemmoscleres of the fossil sponge with those occurring in a number of species of the recent genus *Radiospongilla* Penney and Racek (Fig. 3a-g), the choice of a new genus for this Mesozoic spongillid by the describing authors is fully supported by the present work. In the following section, the fossil sponge's systematic and phylogenetic position will be discussed in the light of recent taxonomic, ecological and geological studies.

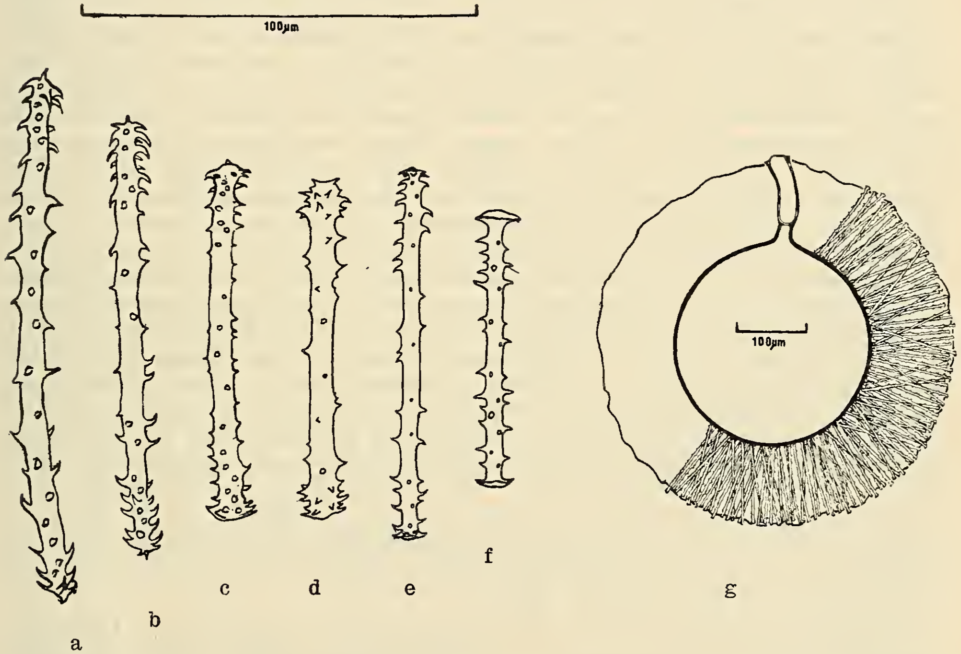

Fig. 3. Morphological features of extant *Radiospongilla* spp. gemmoscleres. a. *R. cerebellata*. b. *R. philippinensis*. c. *R. hemephydatia*. d. *R. sceptroides*. e. *R. crateriformis*. f. *R. cantonensis*. g. Optical section through gemmule of *R. cerebellata* (left half of gemmoscleres omitted).

Systematic, Phylogenetic and Ecological Evaluations

Penney and Racek (1968), by introducing a new genus, *Radiospongilla*, as a natural morphological link between the spongillids with acerate and those with birotulate gemmoscleres, demonstrated the fallacy of the previously widely applied division of the family Spongillidae into the meaningless subfamilies Spongillinae and Meyeninae. Although lacking fossil evidence, Penney and Racek suggested that the two different types of gemmoscleres present in these artificial subfamilies had resulted from divergence from shapes originally present in an hypothetical stock, from which the extant genus *Radiospongilla* could also have evolved. While most species of *Radiospongilla* possess distinctly acerate gemmoscleres, whether of amphioxeous or amphistrongylous shape, they are characteristic in having terminal aggregations of gemmoscleral spines, often forming pseudorotules. One of these species, i.e. *R. cantonensis* (Gee) (Fig. 3f), produces almost perfect birotulate gemmoscleres which are straight and therefore strictly radially arranged, thus documenting the likelihood of a gradual evolutionary divergence of both acerate and birotulate spicules from scleres present in an ancestor, from which both these types could have been derived. The antiquity of the extant genus *Radiospongilla* has now been established by palaeolimnological examinations of Pliocene and Pleistocene sediments (Racek, 1969) and there is no doubt that this genus occupies a central phylogenetic position. However, what could have been more gratifying than to obtain palaeontological evidence of the existence of an even earlier spongillid, which clearly displays ancient traits from which both acerate and birotulate gemmoscleres could have arisen ?

As can be expected from a fossil of about 100 million years of age, *P. chubutensis* differs in several ways from any presently living genus or species. It thus deserves a taxonomic status of its own, at generic as well as specific level, although lying close to *Radiospongilla.* At the same time, the Mesozoic fossil displays spicular and constructional criteria which are now found separately in species of three extant genera, i.e. *Radiospongilla*, *Spongilla*, and *Pectispongilla.* With *Radiospongilla* the fossil shares almost unchanged gemmular and gemmoscleral characteristics and at least one type of megascleres, i.e. those which are incipiently spined, but differs by the presence of free microscleres, which are typically absent in *Radiospongilla. Spongilla*, too, seems to have inherited some of the characteristics of *P. chubutensis.* These are in particular the flesh spicules, of which only the spined type is retained in *Spongilla*, and also the cylindrical shape of the smooth megascleres. Even though *Spongilla* must be considered more distantly related to the fossil than *Radiospongilla*, especially with respect to gemmular and gemmoscleral structure and shape, its evolution from this ancestral type is most likely. *Pectispongilla*, an extant genus closely related to *Radiospongilla*, usually possesses two types of flesh spicules, and thus shares an apparently important morphological criterion with *P. chubutensis. Pectispongilla*, in addition, displays a similar skeletal construction and rather insignificant depths of encrustations. However, although the gemmoscleres are inserted in a manner similar to that both in *P. chubutensis*, and in almost all *Radiospongilla* spp., the gemmules of *Pectispongilla* are much smaller, lack the thick pneumatic coat, and their gemmoscleres display a unique and specialised arrangement of mostly unilateral spines.

As with all fossil evidence, the phylogenetic relationship of the Cretaceous spongillid to living forms can only be assumed until earlier ancestors are found. However, the above comparison of combined characteristics displayed by *P. chubutensis* with those found separately in the three extant genera makes it more feasible to speculate about the possible pathway of spongillid evolution during the past 100 million years, both chronologically and spatially. The fossil clearly demonstrates the early existence of perfected gemmule-producing sponges in inland waters, long before the isolation of non-spongillid Porifera of rather marine facies in the so-called " ancient freshwater lakes ". Recent comprehensive studies by the present authors of a great number of gemmule-less Porifera from a range of thalassoid environments (Racek ; Racek and Harrison, unpublished data) show conclusively that they must have arisen not only from different ancestors but also in much more recent geological times. The polyphyletic origin of the " freshwater sponges ", already assumed by Marshall (1883), commented on by Penney and Racek (1968) and Racek (1969), and discussed by Brien (1966*a*, 1966*b*, 1969, 1973), has thus become well documented.

Until recently, morphological comparisons between fossilised presumed ancestral stocks and extant related organisms were the only means of assessing evolutionary pathways. However, recent continental drift reconstructions from plate tectonics (Oxburgh, 1971 ; Smith, 1971 ; Vine, 1971) can now be used to demonstrate feasible pathways of dispersal and speciation leading from the Mesozoic fossil of Patagonia to related extant groups of spongillids. Since *P. chubutensis* can be recognised as the almost direct ancestral form of the genus *Radiospongilla* in general, and of the *R. cerebellata* group in particular, the present distribution of these essentially southern sponges suggests an evolutionary pathway following a west-east course along the Mesozoic continuity of the combined landmass of parts of South America, Antarctica and Australasia as one route, and along southern Africa and the then connected Indo-Pakistani subcontinent as another. That this is not an isolated case can best be demonstrated by the present range of two different extant spongillids, i.e. *Spongilla alba* and the *Ephydatia ramsayi* complex (Penney and Racek, 1968). While both these extant spongillids display a markedly uniform morphology over their entire range from South America through Australia to at least south-eastern Asia, *S. alba* shows drastic speciation trends from South America northward (*S. cenota* in central America, and *S. wagneri* in the southeastern United States), whereas some distant relatives of the *E. ramsayi* complex (i.e. *E. robusta* and *E. subdivisa*) are not represented south of the United States. Since it has been established (Fooden, 1972) that Australia must have separated from the Antarctic plate some 45–50 million years ago, it is obvious that both *S. alba* and the *E. ramsayi* complex must have existed long before the final dismemberment of " Gondwanaland ". On the other hand, clear speciation trends, and even discontinuity, seem to have occurred along the distributional pathway from South America northward, indicating the earlier existence of major distributional barriers, and ensuing isolation of sponge populations. Another indication of such a development is the absence of the *R. cerebellata* group of sponges, one of the closest descendants of *P. chubutensis*, north of Brasil. In spite of recent detailed studies by specialists in South America, none of the species of the above group have hitherto been recorded from that area, although some more remotely related species are known to range discontinuously from central Argentina Bonetto and Ezcurra, 1964) through Mexico to the United States (Penney and Racek, 1968).

While the evolutionary pathway leading from the Mesozoic fossil to those few most closely related species of *Radiospongilla* now seems well documented, the rise of the extant genus *Spongilla* is more difficult to assume. It consists today of two groups of species, both markedly different in morphological characteristics, ecological preferences and, last but not least, zoogeographic distribution. The *S. alba* complex, already discussed above, must be considered another close relative of *P. chubutensis*, and has a distinct southern distribution and a pronounced preference for alkaline habitats. The geologically more recent *S. lacustris* group appears to be another evolutionary line. It is presently restricted to the Northern Hemisphere, and occurs in acidic to only slightly alkaline lentic and lotic habitats. Although the general morphological criteria within *Spongilla*, as restricted by Penney and Racek (1968), are fairly constant, and certainly generically characteristic, the possibility that these two groups arose separately and at different geological periods cannot be dismissed. Until further fossil spongillids are found, particularly in northern landmasses of the past, any definite conclusions as to the ancestry of the extant genus *Spongilla* s.s. must remain strictly speculative.

In dealing with presumed pathways of evolution and speciation, one naturally has to consider possible dispersal routes. In the family Spongillidae, these do not necessarily require fully connected landmasses, since their gemmules are well known to be distributed by aquatic birds. This often occurs over considerable distances, including extensive stretches of oceans, with occasional dispersal by wind from dried water beds. While such an indirect dispersal could possibly have accounted for the advance of certain spongillid groups from Australia to nearby Asia, or vice versa, the unlikely presence either of true birds or of any other animals capable of intercontinental flight at the time of the occurrence of *P. chubutensis* would seem to rule out such a possibility. Considering all the factors discussed, therefore, the evolutionary advance from the Patagonian fossil to at least those species of *Radiospongilla* which have retained identical gemmular and gemmoscleral structures and characteristics, and which today abound in Australia, Africa and S.E. Asia, can only be suggested to have taken a west-east course prior to the dismemberment of " Gondwanaland ", which would have permanently disrupted such an advance. In the light of this new evidence, the previously held belief that some of the Australian spongillid fauna is a mere southward extension of that of Asia (Racek, 1969), seems severely affected. It is now most feasible to believe that such an advance to both these continents occurred independently, and that any later exchange of certain species from one to the other has been a mutual one.

With respect to ecological evaluations of the probable physical, chemical and climatic conditions present during the occurrence of *P. chubutensis* in the Cretaceous, those characteristic for related *Radiospongilla* spp. may be used for comparison. Both the *R. cerebellata* group of species, and to a certain extent also *R. hemephydatia*, are essentially tropical species. Their conspicuously thick pneumatic coat with its gemmoscleral armature, identical with that found in *P. chubutensis*, is indicative of hot or even arid climates. The two *Radiospongilla* spp. compared above prefer lentic habitats or still backwaters of the lotic series. They furthermore appear to prefer distinctly alkaline conditions in their optimal habitat and show little tolerance of sharp falls in hydrogen-ion concentrations. The thickness of the gemmular pneumatic coat and its dense gemmoscleral armature point to a warm to very warm, and perhaps even arid, climate during the life of the Patagonian fossil in the Cretaceous. Its habitat undoubtedly belonged to the lentic series, as already suggested by Ott and Volkheimer (1972). And the fact that its natural environment must have been strongly alkaline is demonstrated by the abundant, and apparently rapid, growth of the surrounding calcareous algae, as well as by the actual mode of fossilisation.

Zusammenfassung

Der Fund des ersten fossilen Spongilliden, *Palaeospongilla chubutensis* Ott and Volkheimer (1972), aus der Kreide Patagoniens offenbarte interessante morphologische Strukturen, die gründliche systematische und phylogenetische Studien erforderten. Dieses guterhaltene Fossil aus lakustrinen Sedimenten, etwa 100 Millionen Jahre alt, besteht aus zusammenhängenden Skelettfasern von Megaskleren und freien Fleischnadeln, beide vertreten mit zwei verschiedenen Typen. Es enthält ausserdem eine grosse Anzahl von Gemmulae mit deren Belagsnadeln, *in situ*. Die vorliegende Neuuntersuchung dieses mesozoischen Spongilliden warf neues Licht auf die Annahme einer frühen Abzweigung der Gemmulae-erzeugenden Süsswasserschwämme von deren " marinen " Vorfahren. Diese Arbeit beweist, dass *P. chubutensis* als Ahnform dreier rezenten Gattungen, d.i. *Radiospongilla* Penney and Racek, *Spongilla* Lamarck, und *Pectispongilla* Annandale anzusehen ist, da sie kombinierte Nadelformen besitzt, die in den oben genannten Gattungen separat vorkommen, obwohl das Fossil der Gattung *Radiospongilla* am nächsten steht. Die Ergebnisse dieser Untersuchung sind von besonderer phylogenetischer Bedeutung, da sie auf die Abzweigung der früher anerkannten Unterfamilien Spongillinae Vejdovsky und Meyeninae

Vejdovsky von einem zentralen Ahnenstamm hinweisen, der heute durch die spezialisierten Arten der Gattung *Radiospongilla* repräsentiert wird.

Gegenwärtige Fortschritte in den Gebieten der Palaeolimnologie, Plattentektonik, und Kontinentverschiebung werden dazu verwertet, um genauere Unterlagen für die Annahme phylogenetischer Verwandschaftsverhältnisse zu erhalten, und auch die heutige zoogeographische Verbreitung rezenter Arten zu erklären. Es wird ausserdem versucht, die physikalischen, chemischen, und klimatischen Verhältnisse während des Vorkommens des mesozoischen Fossils zu erklären.

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